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INVASIVE HOLLIES (*ILEX*, AQUIFOLIACEAE) AND THEIR DISPERSERS IN THE PACIFIC NORTHWEST

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ABSTRACT

Naturalized *Ilex aquifolium* L. (English holly) was first collected in the Pacific Northwest in 1953, based on herbarium records. Field surveys showed it is now commonly naturalized from northwestern California to coastal British Columbia. *Ilex crenata* Thunb. and *I. opaca* Aiton were also found growing outside of cultivation, but rarely. A key and seed illustrations are provided to distinguish these three *Ilex* species. Between 2003 and 2006 twice-weekly visits to naturalized and cultivated hollies in Seattle revealed seven species of birds disseminating seeds by eating the fruits. American robins, *Turdus migratorius*, accounted for 96% of 2796 frugivory observations on *I. aquifolium*, followed by European starlings, *Sturnus vulgaris* (3.2%). *Ilex aquifolium* fruits ripened in October and persisted for six months, yet 99% of all fruit was consumed between November and February. A study of *I. aquifolium* seed fate found pre-dispersal diurnal seed predation was rarely observed. Bird-regurgitated seed was more frequently attacked by nocturnal rodents in a sheltered forested setting in Clark Co., Washington (39% losses), compared to an exposed urban setting in Seattle (2% losses). The percentage of viable seed surviving rodent attack was higher in the urban sample (66%) than in the forest sample (24%). Commercial and ornamental use of *I. aquifolium* is extensive in the coastal region and less-invasive alternatives should be considered, to provide food and cover for urban avians without degrading natural areas.

Key Words: American robin, English holly, *Ilex aquifolium*, invasive plants, seed dispersal, seed predators, *Turdus migratorius*.

Holly, the genus *Ilex*, is the largest genus of woody dioecious plants, with more than 500 species worldwide (Cuénoud et al. 2000; Loizeau and Spichiger 2004). More than 30 holly species are cultivated in gardens in western North America, as well as a large number of named hybrids (Omar 1994; Galle 1997; Jacobson 2006). No native *Ilex* species are found on the Pacific coast of North America.

Ilex species are recently escaped (a non-native growing outside of cultivation, without human intervention) or naturalized (a non-native growing and reproducing outside of cultivation) in western North America. *Ilex* ovaries ripen into a drupe, usually containing 3–4 nutlets (pyrenes). For convenience, I refer to these ecological dispersal units (diaspores) as fruits and seeds. Little is known about the interactions between *Ilex* species and their seed dispersers and seed predators of the region, although these data can be important for dealing with invasive species. Therefore, in addition to investigating the collection history and distribution of escaped or naturalized *Ilex* species in the region, preliminary studies on holly dispersal biology are reported here: i.e., feeding behavior of frugivorous birds, and seed fate and viability after bird dispersal.

At least eight English birds, including six thrush species, are known to disperse the seeds of English holly, *Ilex aquifolium* L., in its native range (Snow and Snow 1988). Olmsted (2006) reported some unexpected species consuming holly fruit in the Pacific Northwest, such as (American) blackbirds and chickadees. I attempted to reproduce her findings by systematically observing concentrations of fruiting holly species (naturalized and cultivated) in or near Seattle's Washington Park Arboretum over three years, to resolve which birds were responsible for the most frugivory. In the settled landscape of southern England one study found frequent interactions between avian predators and their prey, flocks of fruit-eating birds, which affected fruit-gathering behavior (Snow and Snow 1986). So I recorded the behavior of urban American robin flocks when gathering fruit.

Seed viability and the fate of seeds handled by birds were examined for possible effects of seed predators in two settings: an urban area and in a typical rural forest. I focused on the most widespread and invasive holly in western North America, *Ilex aquifolium*, and asked what species ate the seeds by day, how frequently, and what percentage of seeds were destroyed by seed predators after they were transported by birds. *Ilex aquifolium* seed is protected by a thick bony exocarp (Fig. 1) and germination is delayed 18–36 mo in Europe (Beckett and Beckett 1979; Arrieta and Suárez 2004). For comparison a three-year outdoor seed germination test was conducted in Seattle.

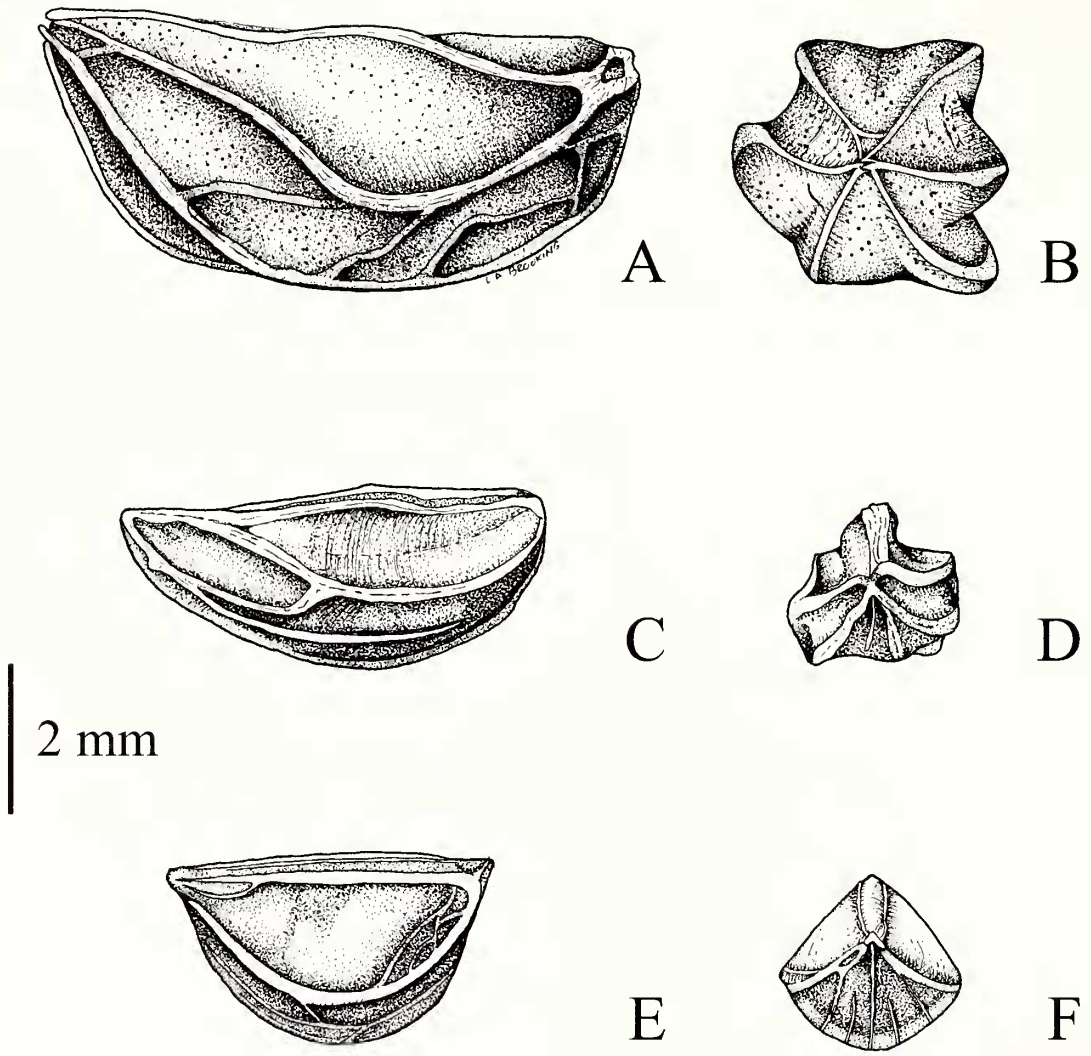

FIG. 1. Seeds of escaped hollies in the Pacific Northwest. *Ilex aquifolium*, (a) lateral view, (b) proximal view. *Ilex opaca*, (c) lateral view, (d) proximal view. *Ilex crenata*, (e) lateral view, (f) proximal view.

METHODS

Distribution

Holly distribution data were compiled from the literature and specimens at the following herbaria: A, BM, CDA, CHSC, COCO, DAV, DAVFP, DBG, DECV, ELRG, FTU, GH, HSC, JEPS, KHD, LINN, MALA, NEBC, NLSN, NY, ORE, OSC, POM, RSA, SCCBC, SFUV, SOC, UBC, UC, UCR, UVIC, V, WILLU, WLK, WS, WTU, and WTUH (acronyms from Holmgren et al. 1990). Additional collections consulted included: the Shasta-Trinity National Forest, Redding, California; Reed College, Portland, Oregon; Olympic National Forest in Olympia, Washington; The Evergreen State College in Olympia; and Fort Clatsop National Memorial, near Astoria, Oregon. The study area was broadly defined as the lowlands west of the Cascade Range in southwest British Columbia, western Washington, and western Oregon. Populations were considered naturalized and mapped if they were obviously not planted and reproducing outside of cultivation, or if herbarium labels indicated they were not cultivated. Field surveys for naturalized holly were conducted on 50 d between 2000 and 2006. Herbarium vouchers from representative naturalized holly populations were deposited at WTU.

Frugivory Studies

The 21 holly taxa in Table 1 were studied at the edge of second-growth forest in the former holly plantings of the Washington Park Arboretum, part of the University of Washington Botanic Gardens in Seattle, King Co., Washington (Omar 1994), or areas within two km of the arboretum, including the University of Washington campus, and the adjacent Montlake neighborhood (Alberti et al. 2001). Frugivory observations were made two times a week during daylight hours between December 2003 and March 2006, while walking to and through the grounds of the arboretum looking for bird activity. All observations of animals eating fruits or seeds were recorded. Individual bird observations began when the first fruit was swallowed and ended when the bird stopped feeding and left the fruit source. It was soon evident that American robins were the most frequent frugivore to visit naturalized *Ilex*, although this aspect of their natural history was not recorded in ornithological literature, so I compiled detailed notes of their feeding behavior. To estimate the transport of fruits and seeds, a count of total English holly fruits swallowed in one feeding bout was made for 25 American robins in Seattle. Ten large robin flocks were also timed (in minutes) when feeding on fruit, starting with the first bird perching on a

TABLE 1. NUMBER OF OBSERVATIONS OF BIRDS SWALLOWING *ILEX* FRUITS IN THE PACIFIC NORTHWEST, 2004–2006. Avians are American robin, European starling (ES), hermit thrush (HT), cedar waxwing (CW), American crow (AC), varied thrush (VT), and northern flicker (NF). Nomenclature follows Andrews (1997).

Ilex	Avian								
	Robin	ES	HT	CW	AC	VT	NF	Total	%
× *altaclerensis* (Loudon) Dallim.	858	87		4				949	19.08
aquifolium L.	2690	90	1	11	2	1	1	2796	56.20
aquifolium × *cornuta*	27							27	0.54
× *attenuata* Ashe	168							168	3.38
× *beanii* Rehder	48		32					80	1.61
ciliospinosa Loes.	20		1					21	0.42
cornuta Lindl. & Paxton	43		1					44	0.88
cornuta × *latifolia* × *pernyi*	95		2					97	1.95
cornuta × *pernyi*	5							5	0.10
crenata Thunb.	40		3					43	0.86
decidua Walter	146			1		1		148	2.98
dipyrena Wall. hybrid	10							10	0.20
integra Thunb.	14							14	0.28
× *koehneana* Loes.	18							18	0.36
latifolia Thunb.	3							3	0.06
maximowicziana Loes.	1							1	0.02
opaca Aiton	338		1	3				342	6.87
pernyi Franch.	37							37	0.74
serrata Thunb.	2							2	0.04
verticillata (L.) A. Gray	163		1					164	3.30
yunnanensis Franch.	6							6	0.12
Total observations	4732	177	42	19	2	2	1	4975	
%	95.12	3.56	0.84	0.38	0.04	0.04	0.02		

fruiting branch and swallowing fruit, ending when the last individual departed. Most frugivory observations were made at close range or with Zeiss 7 × 42 binoculars. Fresh samples of ten fruits were gathered in Seattle and measured for each cultivated species in Table 1 (100 fruits of naturalized *I. aquifolium*), then the seeds were manually extracted, cleaned, counted and measured, to determine the range of fruit and seed sizes and the average number of seeds per fruit.

Seed Predation

Seed predation was detected in several ways. Preliminary study showed birds usually swallowed holly fruits whole and departed, but seed predation was obvious when a bird lingered on the fruiting branch, mashed the fruit in its bill, slowly separating and dropping pulp while extracting, manipulating, and crushing seeds. Squirrels also sat on a fruiting branch, discarding fruit pulp and cracking seeds with their teeth, which was audible from 5 m. Seed predation by birds and squirrels was diurnal, producing small amounts of shredded fruit pulp where they attacked seeds. In contrast, evidence of nocturnal seed predation was indirect. The best evidence came from small gnawed holes in bird-regurgitated holly seeds on the ground, with no adjacent shredded fruit pulp. This was assumed to be (nocturnal) rodents feeding on seed contents; their preference for seeds over fruit flesh shown by untouched freshly fallen fruits within a few cm. Several times in Seattle I saw indications of nocturnal rodents (perhaps a rat sp.) climbing shrubs and feeding on the contents of seeds of *Cotoneaster franchetii* Bois, leaving large amounts of fruit flesh and broken seed husks below the shrub, with many shredded and seedless fruits remaining on the branches. Fruiting hollies were checked for evidence of similar arboreal seed predation by rodents throughout the study, in daylight hours; no direct nocturnal observations of rodents were attempted.

Seed Viability

Seed viability for *Ilex aquifolium* was determined from freshly regurgitated seeds at sites where American robin frugivory was observed along sidewalks and lawn edges in Montlake, Seattle, as well as from second-growth *Pseudotsuga menziesii* (Mirb.) Franco forest near the high school in Camas, Clark Co., Washington. A sample of 500 regurgitated seeds was gathered in Montlake in January 2004, planted in one cm of soil in unirrigated pots left outdoors, and monitored for 3.5 yr to record length of time to germination (Barnea et al. 1991). Additional seeds from the same sites were scored for rodent damage, consisting of a gnawed exocarp and missing embryo. Undamaged seeds were halved with a razor and examined with a dissecting microscope. Grey firm embryos were scored as

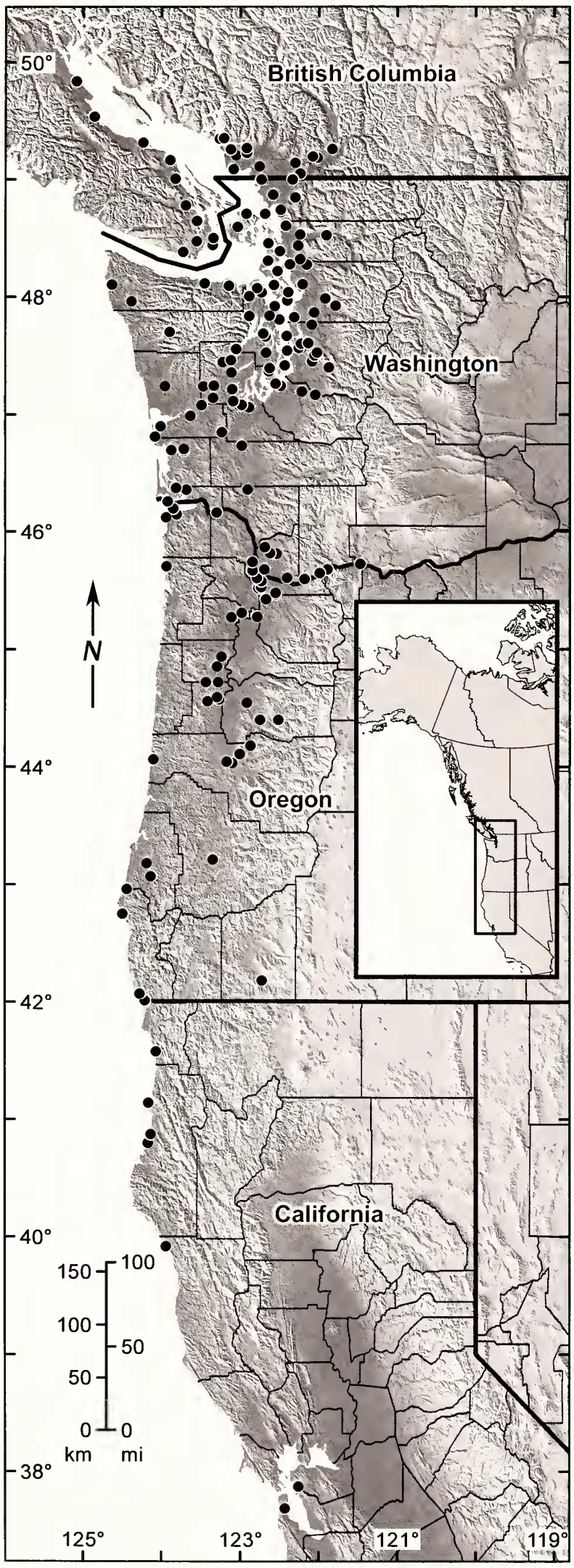

FIG. 2. Distribution map of naturalized *Ilex aquifolium* in western North America, based on herbarium specimens. A few records extend beyond the map boundaries, to the north tip of Vancouver Island in British Columbia (50°35′N, 126°56′W; *Zika 22740* V), and south to Monterey Co., California (36°36′N, 121°54′W; *Zika 23683* RSA).

viable seeds. Liquid, discolored, blackened, or absent embryos were scored as inviable seeds.

RESULTS AND DISCUSSION

Distribution

Literature, herbarium records, and field observations showed three holly taxa escaped from cultivation in northwestern North America: *Ilex aquifolium* (English holly), *I. crenata* Thunb. (Japanese holly), and *I. opaca* Aiton (American holly) (Zika and Jacobson 2005). Their seeds are illustrated in Fig. 1. A key is provided to separate them.

Key to *Ilex* Growing Outside of Cultivation in the Pacific Northwest

1. Leaves less than 30 mm long, less than 15 mm wide, minutely dentate, never spiny; fruit black, 4.8–6.5 mm diam.; seeds nearly smooth . . . . . *I. crenata*
1′ Leaves more than 40 mm long, more than 20 mm wide, entire or spiny-margined; fruit red, 7–13 mm diam.; seeds grooved and strongly ridged
   2. Fresh leaves scarcely shiny or dull above; pistillate flowers solitary and scattered on the twig . . . . . *I. opaca*
   2′ Fresh leaves glossy above, pistillate flowers clustered on short spurs, in subumbels of 1–8 . . . . . *I. aquifolium*

Only *Ilex aquifolium* was abundant enough to represent a conservation concern in the Pacific Northwest; the other hollies were documented as escapes at just one location each. *I. opaca* was vouchered from a single escaped sapling in King Co., Washington (*Zika 20447* WTU). *Ilex crenata* was restricted to two small shrubs on a brushy pondshore in Snohomish Co., Washington (*Zika 20423 & Jacobson* WTU). *Ilex* × *attenuata* Ashe (*I. cassine* L. × *opaca*) was collected as an escape once in 1977 in Sacramento Co., California (Hrusa et al. 2002), but was not recorded escaped in the study area, even though it fruits in cultivation in Seattle.

In the Pacific Northwest I found *Ilex aquifolium* was thoroughly naturalized at low elevations west of the Cascade Range (Fig. 2). I found it reproducing outside of cultivation at hundreds of locations, including forests of all age classes, dominated by *Picea sitchensis* (Bong.) Carrière, *Pseudotsuga menziesii*, *Acer macrophyllum* Pursh, *Alnus rubra* Bong., or *Populus balsamifera* L. subsp. *trichocarpa* (Torr. & A. Gray) Brayshaw. English holly varied from infrequent to common

TABLE 2. MONTHLY FRUGIVORY OBSERVATIONS FOR *ILEX AQUIFOLIUM*, 2004–2006.

Avian	Oct	Nov	Dec	Jan	Feb	Mar	Apr–Sept	Total	%
American robin	7	314	632	872	862	2	1	2690	96.21
European starling		23	51	11	5			90	3.22
Hermit thrush					1			1	0.04
Cedar waxwing					5		6	11	0.39
American crow					2			2	0.07
Varied thrush					1			1	0.04
Northern flicker				1				1	0.04
Total observations	7	337	683	884	876	2	7	2796	
%	0.25	12.05	24.43	31.62	31.33	0.07	0.25		

in fencerows, thickets, roadsides, lakeshores, and floodplains. The majority of naturalized plants were found in rural, suburban, or urban woodlots, fencelines, and hedges, where nearby pistillate cultivated plants provided a seed source. Plant density was highest in some urban greenbelts, with young stands of *Pseudotsuga* and an understory dominated by naturalized *I. aquifolium* rather than native shrubs.

Ilex aquifolium Collection History

English holly was introduced to the Pacific Northwest as an ornamental by 1869 (Ticknor 1986). Fruiting boughs were popular yuletide decorations, so by 1891 the species was established in commercial orchards. A regional industry continues to this day, providing an estimated 85% of the world's crop of cut branches, which totaled 300 tons in 1963 (Ticknor 1986). *Ilex aquifolium* was first noted naturalized in the Pacific Northwest by Brayshaw (1960) and Taylor and MacBryde (1977). Plants were apparently uncommon at first and the species was not included in local and regional floras of the time (e.g., Hitchcock and Cronquist 1961, 1973; Szczawinski and Harrison 1972; Creso 1984). The oldest herbarium collection is dated 1953 (Vancouver Is., *M. C. Melburn s.n.* V). Prior collections, such as a 1931 sheet from the Columbia River Gorge (*Yuncker & Welch 3703* NY) presumably represent cultivated plants as their labels do not specifically state they are escapes. English holly was mentioned as a locally frequent garden escape in British Columbia "on south Vancouver Island, [and] less frequent on the lower mainland" (Douglas et al. 1989). Within a decade it was reported as "frequent in southwestern British Columbia" (Douglas et al. 1998), indicating it was spreading rapidly. In California, *I. aquifolium* was absent from state floras (e.g., Munz and Keck 1965; Munz 1968) until recorded from the northern coast by McClintock (1993). A naturalized plant was first collected in 1976 in Humboldt Co. (*Barker 1594* HSC). In treatments of Oregon plants, Peck (1961) and Thilenius (1968) did not include the species. The first Oregon record was collected in 1986 (*Zika 9818* OSC). More recently Gray (2005) noted *I. aquifolium* was naturalized in both disturbed stands and old growth forests at low elevations west of the Cascade Range. My field surveys disclosed *I. aquifolium* was naturalized in every urban area in western Washington, although the first herbarium gathering was only in 1987 (*Carnevali 203* ELRG). *Ilex aquifolium* was also reported naturalized in Hawai'i (Wagner et al. 1999), New Zealand (Williams and Karl 1996), and Australia (Gleadow and Ashton 1981). Olmsted (2006) reported the species naturalized on the coast of New England, but there are no vouchers at NEBC (R. Angelo, New England Botanical Club herbarium, personal communication), and the report is dismissed here as a mistake for native populations of *I. opa*ca.

Frugivore Studies

The hollies studied (see Table 1) have fruits 5–13 mm diam. and seeds 2–5 mm diam. Apparently none were too large to be swallowed by the local frugivorous birds; seven species were observed swallowing the fruits of the 21 *Ilex* taxa, including cultivated hybrids (Table 1). Native birds were the primary consumers of fruit, but 4% of the feeding observations represent introduced European starlings (*Sturnus vulgaris*). Indigenous birds swallowing *Ilex* fruits, in order of frequency, include: American robin (*Turdus migratorius*), hermit thrush (*Catharus guttatus*), cedar waxwing (*Bombycilla cedorum*), American crow (*Corvus brachyrhynchos*), varied thrush (*Ixoreus naevius*), and northern flicker (*Colaptes auratus*). Robins, often flocking in winter, consumed 95% of the fruit of all combined *Ilex* taxa. Olmsted (2006) reported *I. aquifolium* fruits in the Pacific Northwest provide food for, among others, "...blackbirds, mourning doves, finches, chickadees and non-native house sparrow," but did not provide supporting data, and I was unable to confirm her reports in this study. Those birds were common and seen near or in holly during the three years of field observations, but they ignored *Ilex* fruits.

American robins (Table 2) were responsible for 96% of fruit consumption observations for *Ilex*

aquifolium (n = 2690), and accounted for 99% of the frugivory observed on *I. opaca* (n = 338), and 93% of the frugivory observed on *I. crenata* (n = 40). Robins were common year-round residents in all habitats with naturalized *Ilex* (Sallabanks and James 1999). Published literature documents robins eating the fruits of *I. opaca, I. verticillata* (L.) A. Gray, and *I. decidua* Walter (which are important wildlife food in eastern North America, see Martin et al. 1951), but not the other *Ilex* species in Table 1.

These results suggest that pest control programs for non-native birds like rock pigeons (*Columba livia*) and starlings would have a negligible effect on the dispersal of naturalized holly. On the other hand, the data present a strong argument that urban populations of American robins eat a great deal of *Ilex* in their winter diet, resulting in considerable dispersal of seed into urban thickets and woodlots.

American Robin Feeding Behavior

The local movement of *Ilex aquifolium* seed was easily observed when American robins foraged in the study area between November and February (Table 2), before the onset of spring breeding and a shift in diet to consumption of more invertebrates (Wheelwright 1986). Robins typically foraged in loose flocks of 5–75 birds. Part of the flock advanced towards a fruit tree, in stages, finally arriving and feeding rapidly. Returning to one or several prominent arboreal perches to process the fruit, they maintained a predator watch as a group (Howe 1979; Snow and Snow 1986, 1988; Fleming 1988) before returning to the fruit source. I refer to these lookout points as "relay trees." Flock members repeatedly advanced from the relay tree(s) to feed on fruit. Holly berries were taken while perched, or occasionally snatched in flight. A few fallen fruits were consumed on the ground, or snapped with the bill by leaping from the ground to a low branch. Occasionally fruit was carried away in the bill, and either swallowed or dropped from a new perch.

On *Ilex aquifolium*, feeding bouts for individual American robins in flocks averaged 44 sec, with a range of 10–115 sec. A sample of 100 English holly fruits gave an average of 3.9 seeds per fruit. My observations of 25 robins feeding on *I. aquifolium* gave an average of 5.2 fruits swallowed, or an estimated 20.3 seeds (3.9 seeds/fruit × 5.2 fruits = 20.3 seeds) per feeding bout. *Ilex aquifolium* has relatively large seeds, 5–8 mm. Presumably most were regurgitated within ca. 15 min and very few seeds were defecated (Murray et al. 1993).

Flocks of foraging robins were observed swallowing large numbers of fruits and seeds. In one observation, as many as 157 robins fed undisturbed over a 30 min period on *Ilex aquifolium*, resulting in removal of an estimated 3187 seeds (20.3 seeds/bird × 157 birds = 3187 seeds). For the flock, this observation represents a potential removal rate of 106 seeds/minute (3187 seeds ÷ 30 min = 106 seeds/minute). In another observation, 122 robins fed on *I. aquifolium* over 20 min before scattering at the approach of their major avian predator, a Cooper's hawk (*Accipiter cooperi*). A similar calculation showed they transported an estimated 2476 seeds, removing approximately 124 seeds/min.

American robin flocks commonly used relay trees 10–50 m from the fruit source. Flock members moved holly seeds to many locations, as some birds varied their approach and departure vectors, or fed on more than one fruit species (Kwit et al. 2004). Winter soils were usually unfrozen in the study area, so some flock members occasionally interspersed frugivory with foraging for invertebrates along brushy edges and in lawns, transferring seeds to additional sites. When a predator alarm was given the birds fled, resulting in some robins carrying seeds 500 m before regurgitation. These observations are consistent with those of Holthuijzen and Sharik (1985), who found flock-feeding birds such as American robins, European starlings, and cedar waxwings facilitated long-distance dispersal of large quantities of seed when present. My observations suggest the variable feeding behavior of American robin flocks, with the use of different relay trees, make them effective dispersers for *Ilex aquifolium* (Schupp 1993; Jordano and Schupp 2000).

Seed Germination, Predation and Viability

Germination of *Ilex aquifolium* seed is delayed 18–36 mo in Europe (Beckett and Beckett 1979; Arrieta and Suárez 2004). Regurgitated seeds I gathered and planted January 2004 germinated 29 mo later. Thousands of regurgitated *I. aquifolium* seeds were found under relay trees in Seattle during the study, and it was common to see American robins regurgitate the seeds after feeding on holly fruits. Seedlings were frequent in these sites. I found regurgitated seeds showed no physical differences from seeds extracted from fresh fruits, as did Meyer and Witmer (1998).

Diurnal seed predation of *Ilex* species was rarely observed in the three years of the study, and is apparently insignificant before dispersal. The seeds of *I. yunnanensis* Franch. were taken from fresh fruits once by a spotted towhee (*Pipilo maculatus*). Similarly, introduced eastern gray squirrels (*Sciurus carolinensis*) fed on *Ilex* fruits in Seattle, loudly cracking open the seeds while discarded pulp accumulated below the tree. Squirrels were seen and heard eating the seeds of *I.* × *altaclerensis* (Loudon) Dallim. (n = 15),

FIG. 3. Rodent seed predation of *Ilex aquifolium*, showing gnawed holes and missing embryo, with mm scale.

TABLE 3. NUMBER OF VIABLE SEEDS OF *ILEX AQUIFOLIUM* AFTER RODENT PREDATION, IN URBAN (SEATTLE, KING CO.) AND FORESTED (CAMAS, CLARK CO.) SITES, DETERMINED BY SECTIONING REGURGITATED SEED SAMPLES.

Seed type	Forest		Urban	
	N	%	*N*	%
Rodent damage	300	39	43	2
Viable	184	24	1403	66
Inviable	285	37	680	32
Total	769		2126	

I. aquifolium (n = 5), *I. cornuta* × *pernyi* (n = 3), *I. decidua* (n = 2), and *I. opaca* (n = 1).

In Spain, Obeso (1998) found evidence nocturnal rodents were climbing trees and taking seeds from fresh *Ilex aquifolium* fruits. I sought similar evidence from nocturnal visitors, such as abundant discarded fruit pulp and gnawed seed cases on the ground directly below numerous slashed and damaged seedless fruits still attached to pedicels on the branches. Diurnal seed predators observed in the study (squirrels and birds) never produced similar displays, they always picked the fruit before removing the seeds. I was able to observe nocturnal rodent damage a few times on fruits of cultivated *Cotoneaster franchetii* in Seattle, but never on holly, although I examined thousands of fruiting holly branches during daylight hours. I did not attempt direct nocturnal observations of rodents interacting with *Ilex* fruits.

In forested settings bird-regurgitated seeds were easiest to find under naturalized pistillate holly trees, as in Europe (Alcántara et al. 2000; Obeso and Fernández-Calvo 2003). Post-dispersal seed predation, evidenced by small gnawed holes and a missing embryo (Fig. 3), was assigned to small nocturnal rodents such as mice (Jones and Wheelwright 1987; García et al. 2005). This type of seed damage differed from diurnal seed predation as practiced by squirrels, which left accumulations of discarded pulp. Squirrels extracted seeds from fresh fruit picked and held in the forepaws, and their damage also differed in that they seemed to crush or crack open *Ilex aquifolium* seeds instead of gnawing small holes in them to remove the embryo. Although they may occasionally do it, I never saw squirrels gather or eat scattered regurgitated holly seeds on the ground. So I scored the damage shown in Fig. 3 as nocturnal, not diurnal, rodent seed predation.

My examination of regurgitated *Ilex aquifolium* seeds in woodland settings and edges invariably showed significant nocturnal rodent predation, as noted in Europe (Smal and Fairley 1982; Obeso 1998; Kollmann and Buschor 2002). Nocturnal rodents damaged 39% of regurgitated *I. aquifolium* seed sampled on the ground near pistillate *I. aquifolium* trees in sheltered forest and forest edge settings in Clark Co. (Table 3). These results are qualitatively similar to studies of *I. opaca* in the eastern United States (Kwit et al. 2004) and *I. aquifolium* in Spain (García et al. 2005; Arrieta and Suárez 2005). In contrast, Seattle's urban walks, lawns, and hedges near cultivated *Ilex* trees had a substantial seed rain that was largely ignored by seed predators, with only 2% post-dispersal seed predation by nocturnal rodents. The general lack of cover and suppressed seed predation together suggest a powerful nocturnal predator influence, possibly urban cats (Crooks and Soulé 1999; Haskell et al. 2001).

A secondary effect on seed viability may also result from the differences in post-dispersal seed predation in forested and urban sites. In the forested sample (n = 769), 76% of the regurgitated seed was either damaged by nocturnal rodents or was inviable (Table 3). In the urban sample (n = 2126), only 34% of the seed was either damaged by nocturnal rodents or was inviable. Said differently, 24% of surviving seed was viable in the forest, compared to 66% in the urban sample. Nocturnal rodents may be able to detect and ignore inviable seed in the forest, and apparently are unable or unwilling to attack viable seed in exposed situations in urban settings. Although these are small samples, the

seed studies suggest post-dispersal seed predation is negligible for bird-disseminated holly seed in cities, and may provide a partial explanation for the relative success of *I. aquifolium* in urban and residential areas (Kollmann 2000).

Conservation and Horticultural Implications

Invasive woody plants in North America raise numerous conservation concerns, altering plant communities and displacing the native biota (Catling 1997; Pimental et al. 2000; Friedman et al. 2005; Reinhart et al. 2006). *Ilex aquifolium* is dispersed by the ubiquitous American robin and colonizes forests, edges, and settlements. It represents a long-term management problem in natural areas (Mack et al. 2000; Reichard and White 2001; Dlugosch 2005). As Temple (1990) and Low (2002) discussed, attempts to control or restrict sale of invasive but popular ornamentals like *I. aquifolium* are not always welcomed by gardeners or distributors. Improved public outreach and education are needed, as are ecologically benign substitutes. Table 1 suggests winter-fruiting *Ilex* alternatives exist in the garden trade. They are attractive ornamentals offering cover and food for winter bird flocks, but are apparently non-invasive, as measured by the lack of herbarium records of plants collected outside of cultivation, and an absence of seedlings around irrigated pistillate plants in gardens or arboreta. These all are in contrast to *I. aquifolium*, with many adventive herbarium vouchers and which produces numerous seedlings in the immediate area of pistillate plants. However, potential hybrid replacements for *I. aquifolium* in Table 1 should be tested for seed viability (perhaps a proxy for invasiveness), and monitored for their capacity to reseed in our climate over a longer period than this study. Nonetheless, some hollies seem to show promise as horticultural options preferable to *I. aquifolium*. These include red-fruited deciduous shrubby species like *I. decidua* and *I. verticillata*, popular with birds in Seattle and in England (Ridley 1930). *Ilex* × *meserveae* S. Y. Hu is a little-known low-growing *I. aquifolium* hybrid (*I. aquifolium* × *rugosa* F. Schmidt) but its fruits were outnumbered and ignored by birds in the study area. Landscapers might instead favor evergreen trees with the form as well as the color of English holly, like *I.* × *koehneana* Loes. (*I. aquifolium* × *latifolia* Thunb.), *I.* × *beanii* Rehder (*I. aquifolium* × *dipyrena* Wall.), and especially *I.* × *altaclerensis* (*I. aquifolium* × *perado* Aiton). The latter accounted for 19% of all *Ilex* frugivory observations, and has the dense growth, bright fruit color, and dark shiny foliage most similar to *I. aquifolium*. From an ornamental, ornithological, and invasive standpoint, *I.* × *altaclerensis* may be the best available replacement, based on my initial results. However, any holly must be rigorously tested for invasiveness, and should be commercially available, before promotion as an alternative to *I. aquifolium* in the Pacific Northwest.

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